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## Energetic Bottlenecks and Other Design Constraints in Avian Annual Cycles<sup>1</sup>

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**SYNOPSIS.** The flexible phenotypes of birds and mammals often appear to represent adjustments to alleviate some energetic bottleneck or another. By increasing the size of the organs involved in digestion and assimilation of nutrients (gut and liver), an individual bird can increase its ability to process nutrients, for example to quickly store fuel for onward flight. Similarly, an increase in the exercise organs (pectoral muscles and heart) enables a bird to increase its metabolic power for sustained flight or for thermoregulation. Reflecting the stationary cost of organ maintenance, changes in the size of any part of the “metabolic machinery” will be reflected in Basal Metabolic Rate (BMR) unless changes in metabolic intensity also occur. Energetic bottlenecks appear to be set by the marginal value of organ size increases relative to particular peak requirements (including safety factors). These points are elaborated using the studies on long-distance migrating shorebirds, especially red knots *Calidris canutus*. Red knots encounter energy expenditure levels similar to experimentally determined ceiling levels of ca. 5 times BMR in other birds and mammals, both during the breeding season on High Arctic tundra (probably mainly a function of costs of thermoregulation) and during winter in temperate coastal wetlands (a function of the high costs of processing mollusks, prey poor in nutrients but rich in shell material and salt water). During migration, red knots phenotypically alternate between a “fueling [life-cycle] stage” and a “flight stage.” Fueling red knots in tropical areas may encounter heat load problems whilst still on the ground, but high flight altitudes during migratory flights seem to take care of overheating and unacceptably high rates of evaporative water loss. The allocation principles for the flexible phenotypes of red knots and other birds, the costs of their organ flexibility and the ways in which they “organize” all the fast phenotypic changes, are yet to be discovered.

### INTRODUCTION

Despite a rather standard design (toothless bill, feather coat, light bones, wings and large pectoral muscles), birds show a staggering inter- and intraspecific variation in life histories. What is of special concern in this paper is a mechanistic yet evolutionary understanding of the seemingly extravagant life-styles of long-distance migrants, birds that seasonally commute between “areas of reproduction” and “areas for overwinter survival” that may be half a world apart. Do individual birds that alternate between some of the coldest and some of the hottest parts of the globe ever reach the limits of vertebrate design?

Here I will examine the progress that was made over the last decade in understanding the role of energetic bottlenecks and other design constraints on the life-histories of long-distance migrating and arctic breeding shorebirds, mainly the large sandpipers of the Charadriiform family Scolopacidae (Piersma *et al.*, 1996c). Initially, our project was inspired by the large contrasts in the migrations of separate populations of shorebirds such as red knots (*Calidris canutus*) and aimed to provide an economic analysis of differences in flight distance and climatic conditions encountered (Drent and Piersma, 1990; Piersma *et al.*, 1991a). Upon starting the research reviewed here, I deliberately chose a focal species that was amenable to experi-

mentation in artificial environments (red knots; see Piersma, 1994). I also selected a species living in relatively simple habitats in terms of the physical (*e.g.*, thermal) and the food resource characteristics (Piersma *et al.*, 1993a; Wiersma and Piersma, 1994).

In the research philosophy of our, and indeed many other laboratories, one cannot but to take “physiology into the field” (Drent and Daan, 1980). Field ecological research without due attention to the external and internal (ecophysiological) constraints on the organisms under study is bound to be evolutionarily uninformative. Similarly, fully controlled physiological studies that are cut off from the messy reality of the outdoors, even of animals with interesting life-histories, are bound only to vaguely inform ecological and evolutionary questions (Willmer *et al.*, 2000). George Bartholomew got it all right when he noted in 1958: “*Since an organism is inseparable from its environment, any person who attempts to understand an organism’s distribution must keep in mind that the item being studied is neither a stuffed skin, a pickled specimen, nor a dot on a map. It is not even the live organism held in the hand, caged in the laboratory, or seen in the field. It is a complex interaction between a self-sustaining physico-chemical system and the environment.*” (Bartholomew, 1958).

### FLEXIBLE PHENOTYPES AND LIFE HISTORY EVOLUTION

In a world where adult birds only have fixed traits, it is relatively simple to explain these very traits. For example, heritable variations in beak size can be linked to measures of feeding performance and variations in survival, and thus the evolutionary responses to direc-

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tional selection by variations in environmental conditions can be understood (e.g., B. R. Grant and P. R. Grant, 1989; P. R. Grant and B. R. Grant, 2000). Yet, the aspects of life histories of long-distance migrants that cry out for explanation have to do with the near-continuous *intraindividual* phenotypic changes of these birds, rather than with *interindividual* variation, i.e., their phenotypic plasticity in the more narrow sense (Fig. 1; Piersma and Lindström, 1997). Sequential occurrences in different climate zones, storage and depletion of fuel loads, and drastic changes in plumage, are all aspects of the typical flexible adult phenotype of avian migrants. As the question of whether such animals face energetic and other bottlenecks is obviously connected to the flexibility of morphological structures responsible for energy acquisition, storage and expenditure, I will explain at some length how one can think about avian life history structures, before examining the existence and the role of bottlenecks in avian annual cycles.

Any "life history" is written in the genes, is expressed in the phenotype, and is evolutionary evaluated in the "demotype" (Fig. 1). The hierarchy of "life history structures" and their transformations are inseparable from each other and only exist with reference to the environmental context (Ricklefs, 1991). It is the avian *phenotype* that is hardest to "catch." It is composed of fixed traits (e.g., gender, beak size, skeletal dimensions) and many flexible morphological and behavioral traits as well (Dykstra and Karasov, 1992; Piersma and Lindström, 1997; Starck, 1999b). Phenotypic plasticity is defined as the capacity of single genotypes to produce a variety of phenotypes, but is usually used with reference to the irreversible variation in fixed adult traits (e.g., Travis, 1994). This variation comes about during development as a consequence of variation in the environment by the action of reaction norms (Schlichting and Pigliucci, 1998).

As will become clear below, the size of guts and other metabolic organs provides an example of a truly flexible adult trait. The flexible phenotype of individuals (single genotype, single phenotype as far as the fixed traits are concerned) also encompass cyclical phenotypic variation named "life-cycles stages" by Jacobs and Wingfield (2000). Life-cycle stages specifically refer to seasonally-structured sequences of "unique" phenotypes with respect to state (reproductive or not; molting or not) and appearance (nuptial plumage or not). Both aspects of the flexible phenotype may be under the influence of endogenous programs, especially of the circannual clock system (Gwinner, 1986). Whereas the phenotype is something that one can measure on an organism independently of the environment, the "ethotype" has no meaning except in an environmental context (Ricklefs, 1991, personal communication). Ethotype would include the energy requirements of an individual as a measure of the performance of an individual in its environment (e.g., Burness *et al.*, 2001). To further explain the difference between pheno- and ethotype, and with reference to

what will follow, Basal Metabolic Rate (BMR) would be part of the (flexible) phenotype, whereas the daily energy expenditure (that depends on activity patterns, weather, degree of shelter found, etc.), would be an expression of the ethotype.

All these quantitative phenotypic traits are likely to be under genetic control and the fitness of their variants (the "demotypes," a function of both ecological interactions and sexual selection processes) can be studied (Nager *et al.*, 2000). Fitness determines which of the competing "units of sequenced structures and transformations" (i.e., organisms) will survive in nature's unending struggle (Fig. 1). Many of the design solutions shaping life histories will result from particular allocations of resources (energy, nutrients, time, space) and thus show great interdependence. As a consequence, it will usually be very hard to study the fitness consequences of phenotypic variants with respect to single aspects directly (i.e., by way of demographic studies; but see Ketterson and Nolan, 1992). Instead, a more indirect approach using optimization criteria can help us understand how particular architectural solutions shown by a particular phenotype may evolutionarily have come about (Arnold, 1988; Ricklefs, 1996; Kozlowski, 1999). Although there are many constraints on phenotypic evolution (e.g., constraints resulting from inheritance, selection and development; Arnold, 1992), I will concentrate on the limits imposed by design and assume that phenotypic traits are shaped continuously by natural selection.

#### ENERGETIC BOTTLENECKS AND OTHER DESIGN CONSTRAINTS

Many authors have argued that organisms may face energetic bottlenecks some times during their life, and that such bottlenecks may provide major selection pressures in life history evolution (Kendeigh, 1949; King, 1974; King and Murphy, 1985; Goldstein, 1988; Bryant and Tatner, 1991; Ricklefs, 1996; Bryant, 1999), including winter distribution (Root, 1988). At some level, energy intake (Kirkwood, 1983), digestion, absorption, transport and delivery to the organs will always be constrained by design (Karasov, 1986; Weiner, 1992), and additionally depend on the characteristics of the food (Zwarts and Dirksen, 1990; Kersten and Visser, 1996). The expression of a hierarchy of bottlenecks (nicely visualized as "funnels" by Weiner, 1992) quite easily leads to the concept of symmorphosis: that the limitations in the successive parts of this chain of energy delivering funnels are adjusted to each other in such a way that none is more constraining than the other (Weibel *et al.*, 1998; Weibel, 2000).

There may also be limits to the body size of the organism. It probably depends, among other things, on the mode and medium of transport of the organism (Alexander, 1998). For example, marine mammals are much larger and have much greater energy storage capacity than birds. During long-distance flights birds may run out of fuel if favorable tailwinds are unavail-

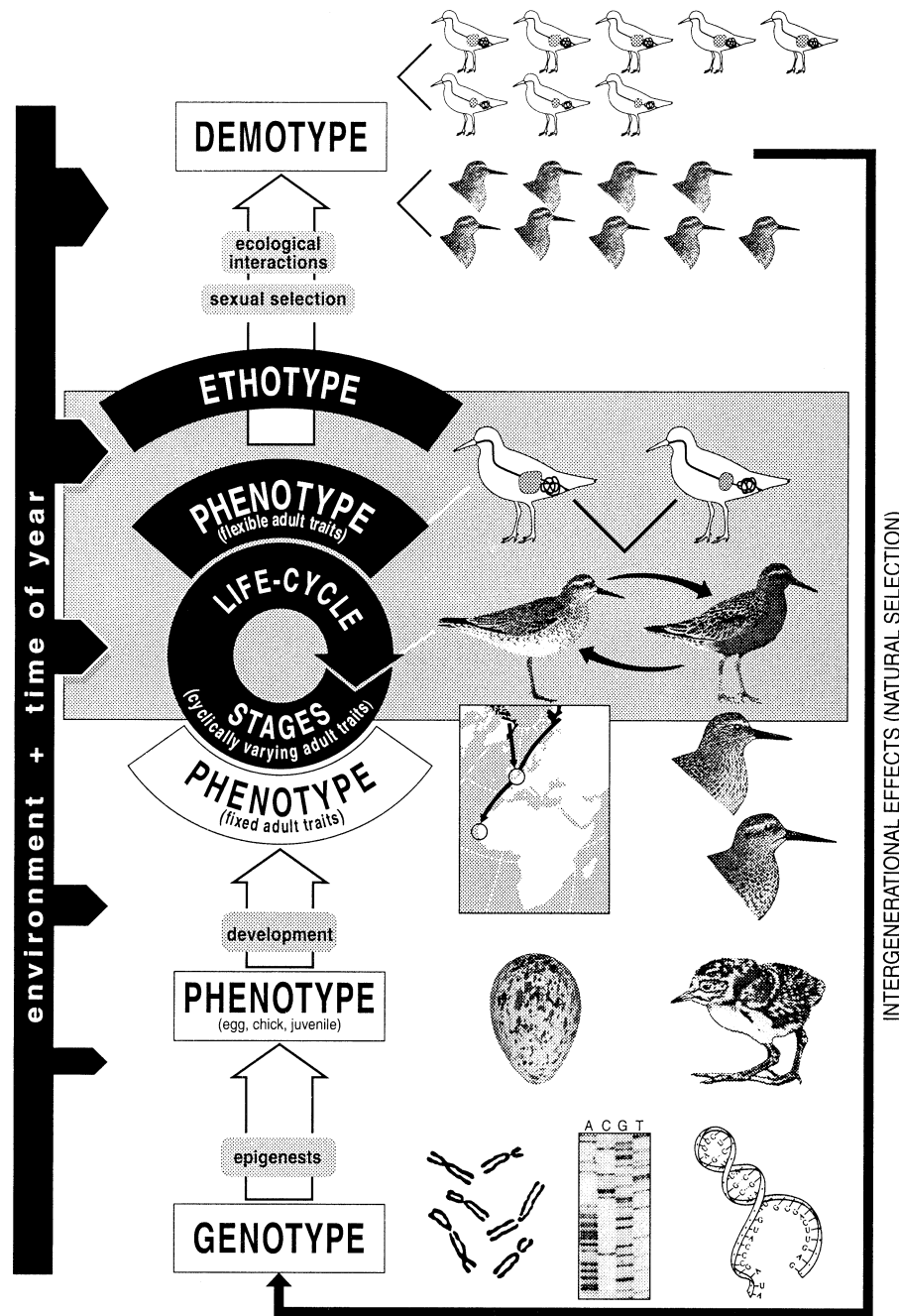


FIG. 1. The "life history" of an animal (in this case of a red knot, a long-distance migrant shorebird) can be regarded to consist of various intragenerational stages (indicated here by the terms genotype, phenotype, and others) in the course of which the influence of environment and time of the year increases all the time. The life history that is most successful under the environmental conditions that an animal happens to encounter, yields the highest numbers of offspring in the next generation (*i.e.*, the most common "demotype," the life history with the highest fitness). The sketches on the right illustrate the phenomena referred to by the *genotype* (chromosomes, part of a DNA sequence and the double helix), the early *phenotype* (egg and freshly-hatched chick), aspects of the adult *phenotype* that are fixed and that are flexible (migration from Canada to Europe versus Siberian to Africa; short- versus long-billed birds, and large- versus small-gutted birds, respectively), including aspects of the phenotype that vary predominantly on a seasonal basis (*life-cycle stages* such as seasonal changes in plumage). Traits that can only be described in relation to environmental conditions are indicated by the term *ethotype* (for example, a trait like daily energy expenditure). The resulting reproductive success of such genetically instructed types is called the *demotype* (in this case illustrated by different numbers of short- and long-billed birds, or of large- and small-gutted birds). The shaded part of this avian life history is the focus of this paper.



able, and thus experience energetic bottlenecks during the flight part of their migration. The rate of energy generation and expenditure may also provide bottlenecks. Rates of heat generation and loss, and rates of work, may simultaneously constrain organismal options. Indeed, such limitations are implicit in the concept of maximum sustained working levels or "metabolic ceilings" (Drent and Daan, 1980; Peterson *et al.*, 1990; Suarez, 1996; Hammond and Diamond, 1997). Here again the question arises whether limitations in energy intake and assimilation (central limitations) or limits to energy expenditure (peripheral limitations) ultimately determine the metabolic ceiling, or whether one would expect these opposing elements to be exquisitely balanced (Hammond and Diamond, 1997). If they are not, organisms would be designed in rather wasteful ways.

The allocation of time to activities with different energy cost and benefit levels may also provide a constraint on what animals can do. To avoid energy deficits, the energy gained during the portion of time spent foraging must equal or exceed the costs incurred by the summation of the various daily activities (Clark and Ricklefs, 1988; Ricklefs, 1991; Tinbergen and Verhulst, 2000).

In addition to such problems of allocation (of time, of space, and of energy), the issue of *marginal values* is critical to energetic bottlenecks (Perrin, 1992). At the most basic level, constraints must occur because the fitness costs of additional investments in a structure or an activity are not outweighed by the pay-offs. For example, the nutritional rewards of a larger or a more effective gut may not outweigh the construction and maintenance costs of such a gut (Sibly, 1981; Diamond, 1991). Animals that spend a greater share of the day eating than others that eat for a shorter period may be able to lift a particular metabolic ceiling (Kvist and Lindström, 2000), but may incur other fitness costs. This phenomenon has been demonstrated with respect to reproductive investments in European kestrel *Falco tinnunculus*, where greater parental effort and energy expenditure to produce higher quality or more offspring at some point no longer offset the fitness costs to the parents themselves due to reduced survival (Deerenberg *et al.*, 1995; Daan *et al.*, 1996).

The "other design constraints" referred to before are of a decidedly ecophysiological, but not of an energetic character. Nevertheless, they may be intimately related to the energetic bottlenecks discussed so far. What I have in mind are limitations to the rates of tissue transformation that may be necessary to accommodate the changing selection pressures on the ethotype in the course of the year. In addition, Jacobs and Wingfield (2000) envisaged that there might be constraints in the endocrine control systems that could limit the speed of changes between life-cycle stages (see also Mrosovsky, 1990), and perhaps even put a limit on the overall complexity of life cycles.

#### THE CASE OF THE RED KNOT: TROPHIC AND IMMUNOLOGICAL SPECIALIZATIONS NECESSITATING LONG-DISTANCE MIGRATION?

The prime example in the ensuing discussions on bottleneck phenomena in avian annual cycles is the red knot, a large sandpiper of the scolopacid family (Piersma *et al.*, 1996c). For this species we have a sufficient body of observations not only to describe the intra-specific variation in annual cycles in great detail (Piersma and Davidson, 1992), but also to formulate hypotheses as to why individual red knots might require half a world to make a living.

Red knots weigh about 120 g when lean, to over 220 g when fully fueled up, and have a circumpolar breeding distribution. They only breed in the most northern and barren types of high arctic and alpine tundra. From these polar desert tundras, different populations migrate southwards to specific overwintering destinations at more southern coastal areas (Piersma and Baker, 2000). The population breeding in the Canadian Arctic (*rufa*) migrates as far as the subantarctic coast of Tierra del Fuego, another (*rogersi*) migrates between Chukotka Peninsula and New Zealand. Of the two populations that will be the focus here, one breeds on tundra in northern Greenland and northeast Canada and winters at temperate latitudes in Western Europe (*islandica*), and the other breeds in northcentral Siberia and overwinters in the tropics of West-Africa (*canutus*). Surprisingly, this whole flyway system may be of post-Pleistocene origin. Studies on allozyme variation and the sequence variation in the rapidly evolving parts of the mitochondrial DNA suggest that red knots survived a population bottleneck some time within the last 30,000 yr (Baker *et al.*, 1994; Baker and Marshall, 1997).

Nonbreeding red knots always are found in coastal wetlands with extensive intertidal mudflats (Piersma, 1994). The scarcity of such habitats dictates that such sites not only are "few," but also "far between" (van de Kam *et al.*, 1999). Thus, the migratory travels from breeding to wintering area and *vice versa* usually involve a few very long-distance flights that routinely measure more than 2,000 km, but may be up to 8,000 km long (Dick *et al.*, 1987; Piersma and Davidson, 1992; Nebel *et al.*, 2000).

On the tundra red knots eat a variety of surface arthropods and spiders (Tulp *et al.*, 1998). During the rest of the year they live on a diet that largely consists of mollusks (Prater, 1972; Piersma, 1991; Alerstam *et al.*, 1992; Zwarts and Blomert, 1992; Piersma *et al.*, 1993a, b, 1994; González *et al.*, 1996). Red knots are well equipped for a molluscan diet as their digestive tract consists of a large muscular stomach for crushing hard-shelled mollusks and an intestine that is able to withstand the stresses of rapidly passing shell-fragments (Dekinga and Piersma, 1993; Piersma *et al.*, 1993c, 1999b). Buried bivalves very often dominate the diet, and red knots are most proficient in their detection (Piersma *et al.*, 1995b). Whereas snipes and

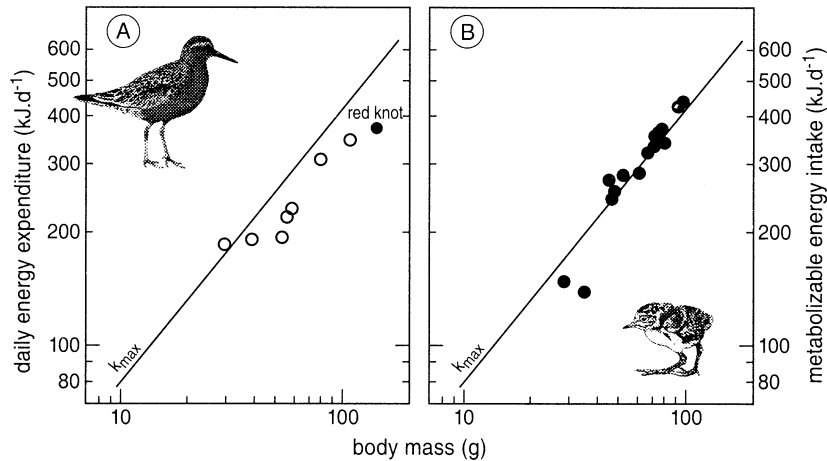


FIG. 2. The cost of high arctic life illustrated by the daily energy expenditure of fully grown adult arctic-breeding shorebirds of different species in the incubation phase (A) and the daily metabolizable energy intake of growing red knot chicks (B), both plotted as a function of body mass. The interspecific data in (A) refer to daily energy expenditures based on *ca.* 24 hr doubly-labeled water measurements of birds captured and recaptured on the nest (from T. Piersma *et al.*, unpublished data); the intraspecific data on metabolizable energy intake rates in (B) refer to energy intake rates calculated by summation of energy expenditure measured by doubly-labeled water and individual increments in energy content (from H. Schekkerman *et al.*, unpublished data).  $k_{max}$  is the allometric approximation of the absolute maximum rate of energy turnover of fully grown birds and mammals according to Kirkwood (1983).

many small sandpipers are equipped with a bill-tip organ to detect the vibrations of subsurface crawling prey (Gerritsen and Meijboom, 1986), red knots may be unable to feel such vibrations. Instead, they are able to detect the presence of static objects such as mollusks buried in soft sediments by the Herbst-corpuscles in their bill-tips which may perceive pressure gradients actively formed by the probing bill (Piersma *et al.*, 1998). On the tundra, red knots rely on keen eyesight to make a living on surface arthropods.

Their food-finding specialization may explain the use of intertidal habitats outside the breeding season, but why would red knots be restricted to the most northern and inhospitable tundra during breeding? Perhaps high arctic tundra as well as open seashores represent relatively parasite- and pathogen-poor habitats where small investments in immunomachinery suffice (Piersma, 1997). Red knots and other high-arctic breeding and long-distance migrating shorebirds may be specialized in having a low capacity of, and/or allocating small nutritional investments to, immunocompetence (Piersma, 1997).

#### "STEADY-STATE" ENERGETICS

##### *The High Arctic breeding grounds*

Is the thermal environment of the High Arctic breeding grounds of red knots, and indeed most other coastal wintering shorebird species, costly, even in summer (Drent and Piersma, 1990), and is there evidence that rates of energy expenditure impose a constraint on the distribution of birds or their activity? A study on ruddy turnstones (*Arenaria interpres*) during the incubation phase (Piersma and Morrison, 1994) using doubly labeled water to measure energy expenditure (Speakman, 1997), showed that these 100 g shorebirds routinely expend the equivalent of four times

their predicted BMR. This is quite close to the metabolic ceiling identified by Drent and Daan (1980; and see Kirkwood, 1983; Peterson *et al.*, 1990; Hammond and Diamond, 1997). Most of the variation in the energy expenditure of these turnstones was attributable to variation in the thermal conditions, a function of air temperature, wind and radiation.

These results were confirmed when we compiled the doubly-labeled water measurements from 30 incubating individuals of eight shorebird species that varied in body mass from 28–150 g (Fig. 2A). Rates of energy expenditure, especially in the smallest species, approached  $k_{max}$  (the absolute maximum rate of energy turnover according to Kirkwood, 1983). Doubly-labeled water data for radiomarked red knots, for which the time budgets during measurement periods were known, showed that foraging away from the nest on open tundra is almost two times as costly as incubating the four-egg clutch (T. Piersma *et al.*, unpublished data). Thus, probably as a consequence of the high costs of thermoregulation when foraging away from the nest, tundra-breeding shorebirds appear to incur daily rates of energy expenditure that are among the highest reported in the literature so far.

If the adult shorebirds find it costly to make a living on the tundra in summer, what about their precocial chicks that also have to feed in this open and exposed habitat? We measured energy expenditure using doubly-labeled water in red knot chicks growing up on the coastal tundra of central Siberia (Tulp *et al.*, 1998; H. Schekkerman *et al.*, unpublished data). To arrive at estimates of the daily metabolized energy we added the energy deposited in new tissue based on carcass analyses. The daily metabolized energy scaled with body mass to the power 0.916 (Fig. 2B; H. Schekkerman *et al.*, unpublished data). Variations in chick

growth rate were correlated with thermal conditions as well as the availability of invertebrate prey as measured by pitfall traps. The energy requirement over the 18 day prefledging period amounted to 5,285 kJ. This is 89% above an allometric prediction based on growth rate and fledgling mass in birds (Weathers, 1992, 1996), and is among the highest values reported to date. During the second and third week of life the net energy intake of red knot chicks exceeded the predicted absolute maximum rate of energy turnover for adult birds and mammals (Fig. 2B).

Thus, red knot chicks seem to be able to “break through” an inferred “allometric” metabolic ceiling. Which factors enable them to do so? Red knot chicks on the Siberian tundra grow relatively fast and must achieve high food intake rates, especially during mild weather (H. Schekkerman *et al.*, unpublished data). The 24-hr daylight period is helpful as it maximizes the potential time available for foraging. Perhaps most importantly, the considerable cold-hardiness of red knots during the first week of life enables them to seek less parental brooding than temperate breeding shorebirds species (Beintema and Visser, 1989) and thus to further increase foraging time. Thus, adjustments in metabolic design (cold hardiness) in combination with particular ecological conditions (long days, accessible surface prey) may have allowed these knots to raise their metabolic performance above the ceiling of Kirkwood (1983). This begs the question why the chicks of temperate breeding shorebirds do not increase cold hardiness as well (*e.g.*, by organ size and capacity adjustments) and thus decrease the risk of death during cold days (*cf.*, Visser and Ricklefs, 1995; Visser, 1998)?

#### Wintering at temperate latitudes

These studies on energetics of shorebirds on the breeding grounds indicate that the costs of thermoregulation loom large in their energy budgets. As shorebirds always live exposed in open habitats with little scope for behavioral thermoregulation (*e.g.*, the selection of favorable microhabitats), it seems likely that the costs of thermoregulation would be an important determinant of energy expenditure year-round (Piersma *et al.*, 1991a). Using heated taxidermic mounts under many conditions in the field, Wiersma and Piersma (1994) derived a series of habitat-specific equations to predict maintenance requirement (*i.e.*, BMR plus the additional cost of thermoregulation when standard operative temperatures are below the lower critical temperature; see Bakken, 1992) from three standard weather variables (*i.e.*, air temperature, wind speed, and global solar radiation). Using these equations and public data on climatic regimes in different areas, predictions were made of the average seasonal changes in maintenance requirements of *Calidris canutus islandica* migrating between the Canadian Arctic breeding grounds and the Dutch Wadden Sea wintering grounds, with a stopover in Iceland. In Figure 3 this reconstruction has been expanded to also include the seasonal

changes in maintenance requirements of *C. c. canutus* breeding in Siberia and wintering in tropical West-Africa. This estimate does not include the costs of foraging and prey processing (even though these may partly substitute for thermoregulation costs; Bruinzeel and Piersma, 1998).

The contrast between the two subspecies is remarkable. Whereas *islandica*-knots incur the highest costs in midwinter, *canutus*-knots face the highest maintenance requirements during the breeding season when they reach values for maintenance metabolism of 2.5 W (Fig. 3). This is about 60% of the empirical estimate using doubly-labeled water of the average energy expenditure during the incubation period (Fig. 2A; T. Piersma *et al.*, unpublished data). If, simply for convenience, we use this ratio of total energy expenditure to maintenance requirement (*i.e.*, a ratio of 1.7) as an approximation for the rather similarly costly thermal conditions in midwinter in the temperate zone, what level of energy expenditure would we predict for wintering *islandica*-knots that incur a maximum maintenance requirement of almost 3 W in January (Fig. 3)? Based on 31 yr of weather data, the long-term average overall maintenance requirement for red knots wintering in the Dutch Wadden Sea (September–April) was 2.6 W (Wiersma and Piersma, 1994). This leads to an estimated average total energy expenditure of 4.4 W, or of 5.1 W during the coldest month. As BMR is close to 1 W in wintering red knots (Piersma *et al.*, 1995a, 1996a), such expenditure levels again approach inferred metabolic ceilings of 4–5 times BMR.

A similarly high level of energy expenditure was demonstrated in small sandpipers (sanderlings, *Calidris alba*) wintering on the cold temperate beaches of New Jersey (Castro *et al.*, 1992). Given the red knots' habit of living in large flocks that range over huge areas (Piersma *et al.*, 1993a, 1995a; van Gils and Piersma, 1999), it is practically impossible to obtain direct doubly-labeled water measurements for this species. Instead, we made metabolism measurements on confined individuals living in natural settings, *i.e.*, a small, 7 by 7 m mudflat where they fed on bivalves that they retrieved from the sediment during low tide (Fig. 4; see Piersma, 1994; Visser *et al.*, 2000). During an outdoor experiment when the maintenance requirement estimated from the predictive equations of Wiersma and Piersma (1994), amounted to 1.5 W, the average energy expenditure of four individuals was almost double that, 2.9 W or *ca.* 250 kJ/day (Fig. 4). That the earlier inferred ratio of 1.7 may not be so general is further illustrated by the results of an experiment during which six red knots foraged on an indoor artificial mudflat. Although, at ambient air temperatures of *ca.* 18°C (*i.e.*, approximately the lower critical temperature; see Piersma *et al.*, 1995a) they faced no cost of thermoregulation, their average expenditure was *ca.* 4 W (348 kJ/day), which is 4 times BMR and not far below the metabolic ceiling of Kirkwood (1983).

In this particular trial (indicated by the code “IF-



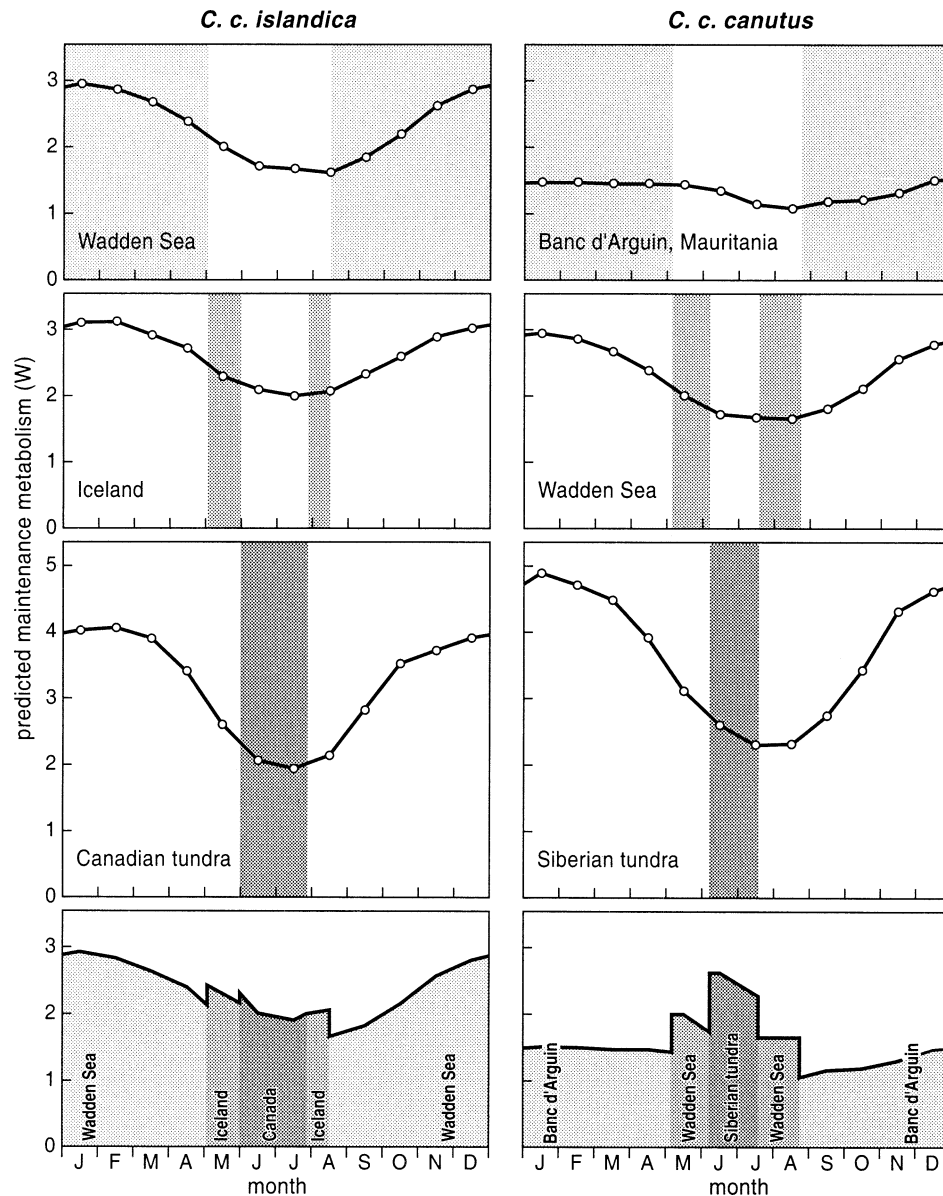


FIG. 3. Comparison of the seasonal variation in levels of thermostatic costs in the Euro-Canadian subspecies *islandica* and the Afro-Siberian subspecies *canutus* of the red knot. The reconstruction for *islandica*-knots is from Wiersma and Piersma (1995).

$C_1$ " in Visser *et al.*, 2000), the birds were feeding on cockles (*Cerastoderma edule*) of very poor quality (*i.e.*, little meat and a lot of water and shell material to take care of in the digestive tract). In this situation the birds had record water fluxes of 625 g/day (which is 17 times the allometric prediction for free-living birds; Nagy and Peterson, 1988). Very high levels of energy expenditure of birds that spent nothing on thermoregulation have to be explained by the cost of crushing the shells and dealing with the huge salt water load (including the dissipation of the salt load by the nasal glands). Although red knots in the wild are expected to feed on higher quality shellfish (more meat per volume of salt water and g of shell) than the ones in this particular experiment, the cost of being a food-specialist with a diet that consists of shellfish ingested

whole will nevertheless always be considerable (*cf.*, Nehls, 1996). We therefore expect red knots wintering in Western Europe to routinely live close to, and often above, the predicted metabolic ceiling of *ca.* 5 times BMR. To cope with such costs, they and other northerly wintering shorebirds have larger nutritional organs than those wintering in more relaxed climates (Piersma *et al.*, 1996a; Summers *et al.*, 1998).

#### Wintering at tropical latitudes

The *canutus*-knots migrating onward to tropical West-Africa are predicted, on the basis of climatic data, to have overwinter maintenance requirements of 1.5 W (Fig. 3). Although they may also face the considerable costs that come with a diet of ingested shellfish, it is unlikely that they approach expenditure lev-



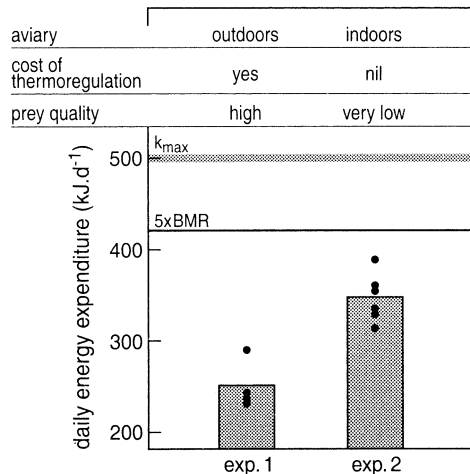


FIG. 4. Comparison of two estimates of daily energy expenditure of shellfish-eating red knots feeding and roosting under natural schedules under semi-natural conditions in (1) an outdoor aviary in April (M. Poot and T. Piersma, unpublished data; see Piersma, 1994) and (2) an indoor aviary (A. Dekinga, T. Piersma, B. Achterkamp, and G. H. Visser, unpublished preliminary data; see Visser *et al.*, 2000).

els of 5 times BMR. Instead, they may face different problems. In tropical environments, especially under conditions of high humidity, the birds may be faced with problems of radiative heat gain (Klaassen and Ens, 1990; Verboven and Piersma, 1995; P. F. Battley *et al.*, unpublished data). Under some conditions internal heat production and the capacity for salt excretion to produce osmotically free water for evaporative cooling may cause birds to hit design constraints that are rather similar to the ones imposed by high thermoregulatory or food-processing costs (Klaassen, 1990; Klaassen *et al.*, 1990; P. F. Battley *et al.*, unpublished data).

In the face of external heat loads it may pay to reduce the internal heat load. Indeed, in congruence with bird species from arid environments that show reduced basal and field metabolic rates compared to birds from mesic environments (Tieleman and Williams, 2000), red knots wintering in West-Africa (Piersma *et al.*, 1996a) and all other shorebird species examined in this climate zone (Kersten *et al.*, 1998), have reduced BMRs compared with shorebirds from temperate winter climates (Kersten and Piersma, 1987). However, before embarking on long-distance flights of many thousands of kilometers, shorebirds usually increase the size of their heart and pectoral muscles (*e.g.*, Piersma *et al.*, 1999c), which may induce increases in BMR (Weber and Piersma, 1996). Simultaneously, the birds develop an envelope of fat, that reduces the capacity of heat loss, and they molt into a darker plumage which increases heat absorption. During such times, there may well be conflicts of phenotypic design.

In the one case study on great knots (*Calidris tenuirostris*) that were near departure on a 5,500 km long northward flight from the humid tropics of northwest Australia (see Battley *et al.*, 2000), such a conflict was

at least in part resolved by behavioral adjustments (P. F. Battley *et al.*, unpublished data). Individual birds that, according to their breeding plumage, were ready to depart showed more extensive heat avoidance behaviors than birds that had not yet molted. This behavior involved the raising of back feathers, a posture that may reduce the external heat load or increase the possibilities for convective or evaporative cooling.

#### TIMES OF CHANGE: MIGRATION

When animals move long distances over inhospitable habitats, they cannot eat and must rely on stored fuels. The time and energy necessary for fuel storage must therefore be considered part of the migration itself (Alerstam and Lindström, 1990; Drent and Piersma, 1990). The ecological issues relevant to migrants during fueling episodes have increasingly attracted specific attention under the banner of "stopover ecology" (Lindström, 1995).

#### Fueling episode

The time required to store the fuel load necessary to cover the distance to the next destination, is determined by the rate of fuel storage (Zwarts *et al.*, 1990). Fuel storage rates could thus provide a bottleneck to avian performance in the same way that rates of energy expenditure may delimit distribution in costly climate zones (Root, 1988). In addition, there is evidence that female red knots also store critical nutrients for egg production such as calcium (Piersma *et al.*, 1996d).

A general demonstration of design constraints affecting refueling was given by Lindström (1991). If there exists a limit to the amount of food that can be processed (an energetic bottleneck of the kind envisaged by Kirkwood, 1983), and if birds at stopover sites require about two times BMR for maintenance and basic activities, then the maximum part of the metabolized energy intake that is theoretically left for fuel storage is about 2–3 times BMR. As mass-specific BMR decreases with increasing body mass (Lasiewski and Dawson, 1967; Aschoff and Pohl, 1970), smaller bird species should be able to put on fat at a higher relative rate than larger birds (Lindström, 1991). Expressed as a percentage of lean body mass per day, the fuel deposition rate should scale to mass with an exponent of  $-0.27$ . This is precisely what the field data show (Lindström, 1991). If a certain relative fat mass yields a certain flight range irrespective of the size of the bird (Pennycuik, 1975), then large species need more time for fueling than smaller species per distance traveled.

One can escape this allometric rule as a species or as an individual by modifying the constraining factors of the design. If a bird could increase the size of the food-processing organs, then it could potentially increase fueling rate (Klaassen *et al.*, 1997). Lindström and Kvist (1995) showed that under *ad lib.* food conditions, species that have a relatively high fueling rate also have a relatively high BMR. A study on refueling

blackcaps *Sylvia atricapilla* demonstrated experimentally that the rate of energy assimilation under *ad lib.* food was proportional to the size of intestinal tract and liver (Karasov and Pinshow, 2000). As will be illustrated below, BMR often appears to reflect the size of the organs involved in the process of food intake and nutrient processing.

However, a powerful gastrointestinal tract is heavy and costly to carry around; it would reduce the flight range obtained per gram of fuel. A “fit” migrant would therefore be expected to vary its capacity for food processing by changing the size and/or capacity of gastrointestinal tract and liver depending on whether it is fueling or ready to start a long-distance flight. Similarly, the “flight machinery” consisting especially of pectoral muscles, heart and blood should increase in size just before departure. This is exactly what recent field studies have found (Piersma *et al.*, 1993c, 1996b, 1999c; Battley and Piersma, 1997; Jehl, 1997; Biebach, 1998; Karasov and Pinshow, 1998; Piersma, 1998; Piersma and Gill, 1998), and what was also shown in experimental settings (Hume and Biebach, 1996; Dietz *et al.*, 1999b; Lindström *et al.*, 2000).

The principle can be illustrated by data on the patterns in fuel storage and organ change of two populations of similarly body-sized red knots during northward migration (*islandica*-knots in Iceland and *rufa*-knots in Delaware Bay). In this example the timing of northward migration is highly synchronized within the population and for this reason it is possible to approximate individual compositional changes by sequential sampling of the populations (Lindström and Piersma, 1993; van der Meer and Piersma, 1994). After arrival from Western Europe in Iceland in early May 1994, no fat is stored during the first week or so, but during this time the liver increases in size (Fig. 5). After this time, fat deposition is in full swing and the organs involved in nutritional processing (intestine and liver) further increase in size (Fig. 5). In the days before departure the sizes of these nutritional organs decrease, and simultaneously the sizes of pectoral muscles and heart increase (Piersma *et al.*, 1999c).

In 1998, a “normal year,” the pattern for *rufa*-knots arriving in Delaware Bay from South America was basically similar to that of the *islandica*-knots in Iceland. An important difference was that the birds in Delaware arrived with smaller fat stores and also a smaller intestine and liver, probably a function of the very long flight from South-America that they just made (Harrington, 1996). During such sustained long-distance flights, loss of proteinaceous material is as much unavoidable as it is strategically convenient (Pennycuik, 1978; Jenni and Jenni Eiermann, 1998; Battley *et al.*, 2000). The intestine of red knots in Delaware Bay in the normal year 1998 did not reach the lean intestine mass of birds in Iceland, which may have to do with the difference in diet: horseshoe crab (*Limulus polyphemus*) eggs in Delaware Bay (Castro *et al.*, 1989) and mollusks in Iceland (Alerstam *et al.*, 1992).

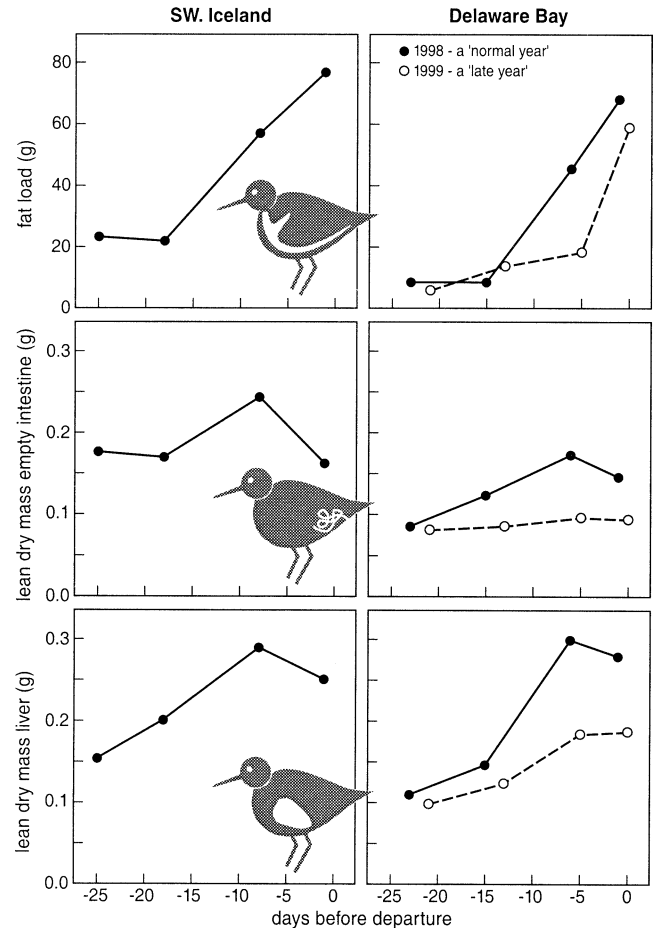


FIG. 5. Changes in the average fat loads and the fat-free dry mass (i.e., the mass of functional tissue) of the empty intestine and the liver in red knots fueling up in Iceland in May 1994 (left panels) and Delaware Bay in May 1998 and 1999 (right panels). The Iceland data are from Piersma *et al.* (1999b) and the Delaware data from T. Piersma, A. Dekinga, and D. B. Carter (unpublished). Dates of departure are 28 May in Iceland and 29 May in Delaware Bay.

In 1999 some red knots arrived in Delaware Bay at normal times and with normal body masses (illustrated by the “first” data point in Fig. 5), but the great majority of birds arrived very late (P.M. González *et al.*, personal communication), mostly only about 10–15 days before the day of northward departure (*ca.* 29 May). These birds were therefore able to start storing fat only about a week before take-off but, surprisingly, they managed quite well (Fig. 5). On the day of departure, fat stores were only a little below the stores in the normal year 1998. Somehow they had been able to compensate time losses by higher storage rates. The surprising fact is that they were able to achieve these very high storage rates with intestines that showed no gross hypertrophy, and livers that showed increases much smaller than in the previous normal year. This suggests that birds increased some other component enhancing fueling efficiency than gross morphological changes, perhaps a reliance on the reserve capacity of the digestive enzyme systems (Diamond and Ham-

mond, 1992; Hammond and Diamond, 1992; Diamond, 1993). Thus, organs such as the liver apparently are capable of doing a "job" even if of smaller size. In turn this implies that there must be a cost to fast fueling with undersized organs. This additional layer of flexibility that showed its face under conditions of severe time pressure, emphasizes once more that bottlenecks are relative.

#### *Evidence for other, "organizational," constraints?*

Between the time red knots and other tundra-breeding shorebirds take-off from the last staging site and fly the several thousand kilometers into the Arctic region to settle on a tundra territory and find a mate, other changes must take place. Not only do they have to shift phenotype with regard to a change from a "fueling" to a "flight" type, they also go from a non-reproductive into a reproductive mode. Red knots already start displaying in the days before departure to the High Arctic (Piersma *et al.*, 1991b), and during the same time they suddenly start making peculiar and complicated diester preen waxes that may play a role in sexual advertisement (Piersma *et al.*, 1999a; Sinninghe Damsté *et al.*, 2000). They also steeply increase baseline levels of the stress hormone corticosterone before departure (Piersma *et al.*, 2000; see Landys-Ciannelli *et al.*, 2002 for the very similar bar-tailed godwit *Limosa lapponica*), and strongly decrease baseline corticosterone some time after arrival on the tundra (Reenerkens *et al.*, 2002). In short, the birds show fast and complicated changes from one life-cycle stage to another, and the speed and accuracy of such changes may be determined by a kind of "reorganization" constraint (*cf.*, Wingfield and Jacobs, 1999; Jacobs and Wingfield, 2000).

#### *Flight episode*

Birds in transit may have to abort their flight as a consequence of running out of energy, water or protein (see Fig. 2D; Yapp, 1962; Carmi *et al.*, 1992; Klaassen, 1995, 1996; Klaassen *et al.*, 1999). In a recent study, Landys *et al.* (2000) intercepted bar-tailed godwits as they were arriving onto their Wadden Sea stop-over site after a 4,300 km migratory flight. No differences were found in the percent body water of arriving godwits compared with those which had already rehydrated. This suggests that these birds were able to maintain physiological water levels during flight.

Although for such long-distance migrating shorebirds, stored energy may thus indeed be the main constraint to flight range (*cf.*, Piersma and Jukema, 1990), empirical measurements of flight costs as a function of the energy store of individual birds have only just begun (Kvist *et al.*, 2001). The finding that the efficiency with which metabolic power input is converted into mechanical power output by the flight muscles increases with fuel load suggests another, hitherto unrecognized, layer of physiological flexibility.

#### RE-EXAMINING THE RELATIONSHIP BETWEEN BMR AND METABOLIC CEILINGS

The recent experimental work on birds and mammals demonstrates that metabolic performance can be increased, by means of phenotypic (organ) adjustments, by cold stress (Williams and Tieleman, 2000), or, in mammals, by the milk demands of increased litter sizes (Hammond and Diamond, 1992; Speakman and McQueenie, 1996), or both (Hammond *et al.*, 1994). The study of Hammond *et al.* (1994) also indicates that a capacity for enhanced thermoregulation is quite different from a capacity for enhanced lactation. Different organ systems seem to provide different constraining factors, which can then be lifted to various extents under increased specific demands.

Confirming the initial hypothesis (Kersten and Piersma, 1987) and the first assessments of this hypothesis using comparative data (Daan *et al.*, 1990, 1991), there is now also ample evidence from intra-specific studies that changes in the size of metabolic machinery (lean mass, size of different organ systems) are reflected in changes in BMR (Table 1), although simultaneous changes in the metabolic intensity of the organs can destroy such relationships (J. A. Gessaman, A. Dekinga, and T. Piersma, unpublished data). Ricklefs (1996) discussed whether maximum field metabolic rate should be seen as a direct function of BMR, or whether these quantities should be treated as energetic consequences of different aspects of an organism's performance. He concludes that the relationship between BMR and field metabolic rate "may be fortuitous rather than direct." On the basis of the foregoing discussion I would claim that the relationship is indeed indirect but certainly *not fortuitous*. BMR reflects the maintenance cost of the metabolic machinery necessary for animals to achieve peak metabolic performances, whether by expending high rates of energy during strenuous exercise (requiring large pectoral muscles and hearts and viscous blood) or whether by storing large amounts of energy rich fuel each day (requiring large guts and livers).

Thus, the graphical model presented by Piersma *et al.* (1996a; see Fig. 6 top) to show how BMR and field metabolic rate would be functionally coupled is incomplete. BMR, in reflecting the size and capacity of the metabolic machinery, does not determine a general ceiling, but by virtue of the size and capacity of particular organ groups rather sets *particular kinds* of ceiling (Fig. 6). Depending on the other costs (*e.g.*, cost of thermoregulation) that an organism has to meet (Klaassen *et al.*, 1997), the size of the digestive machinery could set a limit to fueling rate (Fig. 6). Equally, the size of the exercise organs such as the pectoral muscles and the heart could set a ceiling to a capacity for strenuous exercise and thermoregulation. Although incomplete because of the compartmentalization, the rationale of using BMR as a yardstick to judge maximal sustained metabolic performances (Drent and Daan, 1980; Hammond and Diamond, 1997) is nev-



TABLE 1. Evidence from intraspecific studies that BMR is possibly a function of the size of metabolically active organ systems.

Species	Nature of positive association between the size of organ (groups) and BMR-level	Reference(s)
Mouse	Interindividual correlation between the experimentally varied size of alimentary tract, liver and kidneys and BMR	Speakman and McQueenie, 1996
<i>Mus musculus</i>		
Field vole	Interindividual correlation between heart, kidneys and liver and BMR	Meerlo <i>et al.</i> , 1997
<i>Microtus agrestis</i>		
Red junglefowl	In females, BMR correlates with spleen mass and in males BMR correlates with mass of intestinal tract and lung	Hammond <i>et al.</i> , 2000
<i>Gallus gallus</i>		
European kestrel	Kestrels on restricted diet have lower BMR and disproportionately lower heart and kidney mass than controls	Daan <i>et al.</i> , 1989
<i>Falco tinnunculus</i>		
Great knot	Post-migration and starved birds have lower BMR, correlated with pectoral muscle and intestinal masses	Battley <i>et al.</i> , 2000, 2001
<i>Calidris tenuirostris</i>		
Red knot	Interindividual correlation between size of heart and pectoral muscle and BMR	Weber and Piersma, 1996
<i>Calidris canutus</i>		
Red knot	Red knots with small nutritional organs have a relatively low BMR as well	Piersma <i>et al.</i> , 1996a
<i>Calidris canutus</i>		
Tree swallow	Interindividual correlation between mass of kidneys and hematocrit, and BMR in reproducing adults	Burness <i>et al.</i> , 1998
<i>Tachycineta bicolor</i>		
Hoopoe lark	Liver, kidney and intestine were larger in the cold-exposed group which also had the higher BMR	Williams and Tieleman, 2000
<i>Alaemon alaudipes</i>		
House sparrow	Interindividual correlation between mass of heart, liver, pectoral muscles and lungs on the one hand and BMR on the other	Chappell <i>et al.</i> , 1999
<i>Passer domesticus</i>		

ertheless quite valid as long as the appropriate values for BMR are used. As authors have frequently used single values for BMR and certainly not values that were measured in the hardest-working phenotype (*e.g.*, Peterson *et al.*, 1990:table 3; Hammond and Diamond, 1992; Speakman and McQueenie, 1996), in practice this means that some of the ratios between maximum sustained metabolic rates and BMR will be much too high.

#### GENERAL DISCUSSION

##### *Flexible bottlenecks, ceilings, phenotypes*

Energetic bottlenecks and metabolic ceilings are as heuristically valuable as they are elusive. Nothing is really fixed and unless one verifies ceilings in energy expenditure by experimentally increasing the demands (Hammond and Diamond, 1992; Hammond *et al.*, 1994; Speakman and McQueenie, 1996), it is not possible to say whether an exercising animal could work harder or not. Yet, sometimes rates of energy expenditure are truly refractory to experimental modification. European kestrels and great tits (*Parus major*) with enlarged broods (Masman *et al.*, 1989; Tinbergen and Dietz, 1994; Verhulst and Tinbergen, 1997; Tinbergen and Verhulst, 2000), or European starlings (*Sturnus vulgaris*) that had to work hard for their food (Bautista *et al.*, 1998), were all “unwilling” to expend the expected amounts of energy on the additional labor demanded by the experimental conditions. Instead, they seemed to compromise performance and/or allocated energy intake differently by changing their time budget, body composition, expenditure during periods of rest, or any combination of these factors. Energetic bottlenecks appear to be set by the marginal value of organ size increases relative to particular peak requirements (including safety factors; Diamond, 1993).

Especially in the starling-experiments of Bautista *et*

*al.* (1998), the power of a flexible phenotype seemed to make it impossible for the experimentators to raise the work level beyond 2.5 times BMR, the absolute expenditure level even being lowered during hard work as a consequence of concomitant reductions in body mass and energy expenditure. Thus, it is indeed all a matter of trade-offs and allocations in the light of fitness considerations (Ricklefs, 1996; Bryant, 1999). Nature will not give these engineering rules away easily.

##### *Why can some species live so close to the metabolic ceiling?*

It is striking that all red knots live an energetically costly life-style during some periods of the year, and that some (*e.g.*, *islandica*-knots) almost always are near the theoretical ceiling levels based on studies in a wide range of birds and mammals. Why can such birds afford to be so apparently energetically “wasteful” whereas others seem to be so thrifty (Bryant, 1999)?

Earlier I suggested that the habitats chosen by red knots and related arctic-breeding shorebirds may be relatively disease-free and thus require little investment by animals in immunological defense (Piersma, 1997). Immunological defense may be very costly in survival terms (*e.g.*, due to the production of DNA-damaging free-radicals; *e.g.*, Klasing and Leshchinsky, 1999; von Schantz *et al.*, 1999), just as expending energy is for the same reasons. Germ-poor environments may thus allow their inhabitants energetically costly habits without further enhancing the aging process and reducing survival. Therefore, the lack of damaging immunodefense efforts permits sustained high rates of energy expenditure and physically demanding flights (Piersma, 1997).



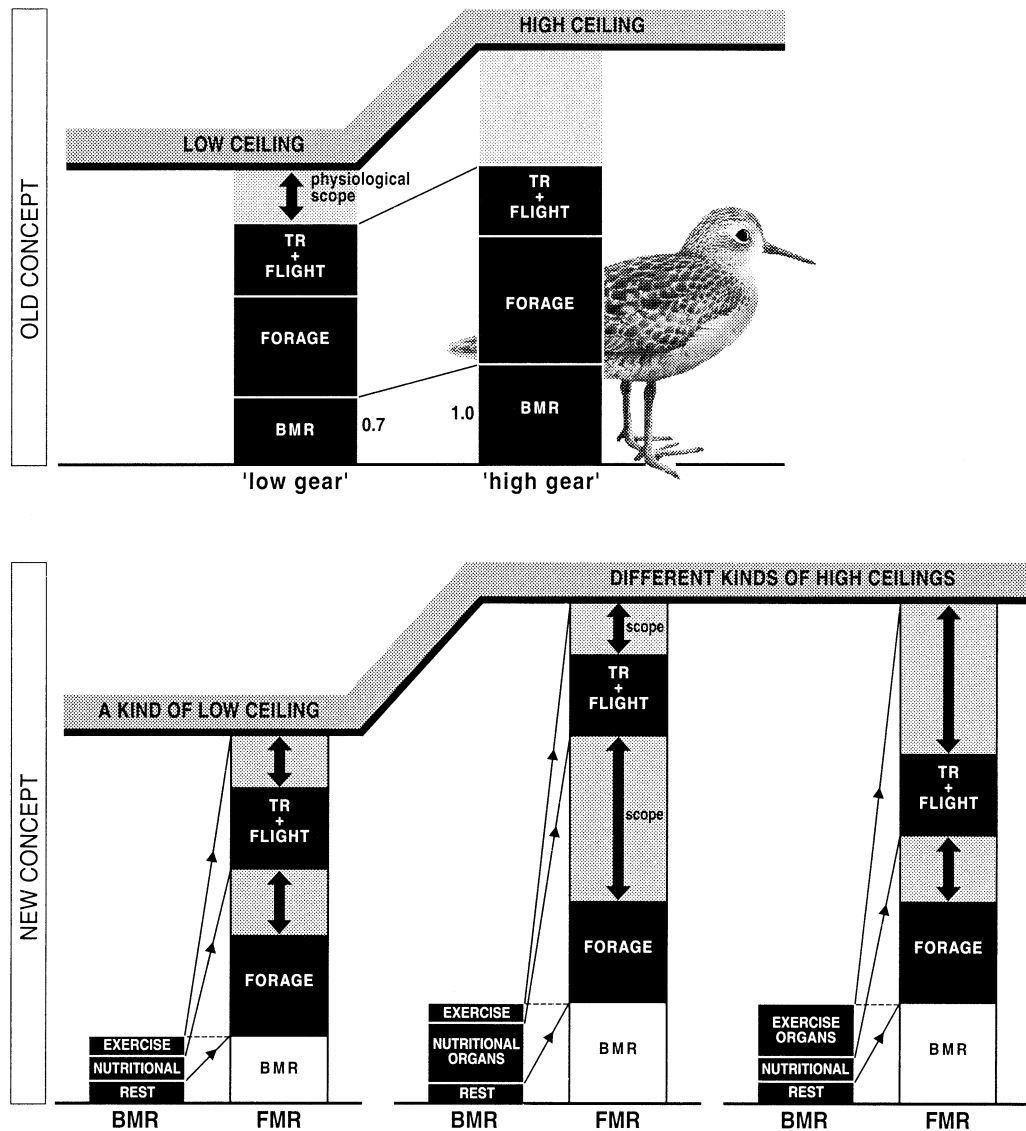


FIG. 6. An old and a new version of a diagram to demonstrate the functional link between the heights of metabolic ceilings and Basal Metabolic Rate (BMR). In the new concept due attention is given to the idea that BMR reflects the summed contribution of size-related maintenance requirements of different organ systems (assuming invariable metabolic intensity). The vertical double-arrows indicate the "scope" for enhanced sustained performance given the size of the metabolic machinery.

#### *New directions in ecological physiology?*

It is remarkable that in the soul-searching enterprise of American ecological and evolutionary physiology in the 1980s (a series of chapters edited by Feder *et al.*, 1987), the statement that "*energy availability and utilization are important constraints on animal function*" (Bennett, 1987) was acknowledged as a hard fact. Yet, the very existence of such "constraints," and the fact that the constraints themselves are nature's solutions to competing demands, remained unexplored in this book except for Futuyma's (1987) question: "*why can't a species adapt enough to spread a little further over an ecological or geographical gradient? ... what are the constraints on adapting further?*" In the book the value of *interindividual* comparisons to gain evolutionary insight in organismal design attract-

ed numerous contributions, but the *intraindividual* variation in morphology and physiology received no attention at all. Ecophysiological studies of long-distance migrant birds have definitely illuminated the fact that ecological and evolutionary pressures can result in remarkable seasonal variation in organismal design. Now that the techniques to assay such *intraindividual* variation, in for example internal morphology and hormonal orchestration, are becoming available (*e.g.*, Wingfield and Farner, 1993; Dietz *et al.*, 1999a; Piersma and Klaassen, 1999; Starck, 1999a), this exciting and perhaps critical layer of organismal complexity is within reach of investigation.

I expect that long-distance migrants will yield some surprises with respect to the physiology of fuel utilization (Guglielmo *et al.*, 1998; Jenni and Jenni-Eier-

mann, 1998, 1999). Some of these may be relevant to human issues like obesity and sport physiology (cf., Secor and Diamond, 1998; Guglielmo *et al.*, 2001). The enormous flexibility in size of critical and complicated organs like the liver may give us insights to the processes of rapid cell proliferation and cell death during ontogeny, cancer and starvation. With respect to disease and aging, studies of the natural history of hard work, energetics, free-radical damage and senescence are already contributing greatly (e.g., Austad and Fischer, 1991; Ricklefs and Finch, 1995). In addition, long-distance migratory birds offer beautiful models when it comes to the virtually unexplored but basic field of the endogenous organization of the seasonal changes in vertebrate phenotypes and ethotypes (cf., Jacobs and Wingfield, 2000).

## ACKNOWLEDGMENTS

Rudi Drent is the muse of the research presented here. He personally took physiology into the field in the 1960s, during a doctoral study on herring gull incubation behavior (Drent, 1970). Ever since he inspired his students to explore similarly profitable avenues of investigation. My own work owes a lot to several other people too. Many of those appear as co-authors of research publications listed below, but I like to specifically mention here Allan J. Baker, Phil F. Battley, Anne Dekinga, Maurine W. Dietz, Petra de Goeij, Jan van Gils, Patricia M. González, Anita Koolhaas, Anders Kvist, Meta Landys, Åke Lindström, Martin Poot, Jeroen Reneerkens, Bernard Spaans, Henk Visser and Popko Wiersma for key contributions. Funding came from many places but was largely taken care of recently by a PIONIER-grant from the Netherlands Organization for Scientific Research (NWO). The Delaware studies in 1998 and 1999 were carried out in conjunction with David B. Carter and James Hewes of the Delaware Coastal Management Program with Sea Grant support. This is NIOZ-publication 3544. The manuscript received important feedback from Phil Battley, Maurine Dietz, Jim A. Gessaman, Åke Lindström, Bob Ricklefs, Hans Schekkerman, Joost Tinbergen, Popko Wiersma, two anonymous reviewers and the organizers of the symposium, Berry Pinshow and David Goldstein.

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